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On the food of green plants.[1]

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The constant tendency of biological science is to minimize the difference between the physiological processes of plants and animals, and to recognize, under the varying forms, a remarkable functional unity. External form and even function were studied long before it was known upon what, in essence, both depended. Dujardin, a zoologist, seeking in 1835 a name for the living matter of which some of the simplest animals were composed, selected the word "sarcode." Von Mohl, a botanist, seeing in 1846, in the cells of some plants, previously unnamed contents which he considered the simplest living material, called it "protoplasm." The acute Payen immediately suspected the identity of these two substances. Cohn in 1850 maintained this identity. But it was not till 1860 that Max Schultz definitely established it. This year 1860 marks an epoch, since modern biology takes thence its rise, thanks to Darwin and Schultz.

Having thus a common starting point in its physical basis, it was natural to expect that the manifestation of life in plants and animals should be essentially similar. Unfortunately, not only in the popular mind are the functions of plants and animals supposed to be radically unlike, but even in many scientific or pseudo-scientific text books they are either specifically or impliedly treated as belonging to totally different categories. And the popular notion is in reality derived chiefly from the text books; although the newspaper article is responsible for much "science falsely so called." This notion apparently depends in part upon the superficial, yet apparently radical, differences between the higher plants and the higher animals, and is deepened by the fact that we are con-

[1]Read before section G, A. A. A. S., Madison meeting, August, 1893.

scious animals and, looking at the plant from our point of view, assume an *a priori* difference.

Since the time of Linnaeus' dictum concerning the three kingdoms—"Minerals grow; plants grow and feed; animals grow, feed, and move"—text book writers, some even of the highest rank, have attempted to define the differences between plants and animals. These alleged differences have been growing fewer and fewer, and it is the purpose of this paper to show that another difference is only superficial, and so to demonstrate more completely the unity in diversity that exists in the physiology of living things.

Among the supposed differences between green plants and animals, none has been more persistently urged than this: Green plants live chiefly upon inorganic food, obtained in the form of CO_2, H_2O, and mineral salts; whereas animals require organic food. This statement is so trite that it is not necessary to cite any specific illustrations in evidence. It is conceded that the nutrition of fungi is essentially animal-like in the character of the food. These organisms require organic substances which have come into solution through physical or chemical causes independent of the fungus, or those which have been dissolved by chemical substances (generally enzymes) secreted by the fungus filaments. In passing it may be remarked that we have in the latter cases a process entirely like digestion in the animal stomach or in the food vacuole. In fact the term digestion, meaning the alteration of foods and their solution preparatory to absorption, is strictly applicable to this process, and ought to be applied to it.

In regard to the food of green plants, it must first be noticed that in a scientific sense the terms organic or inorganic are now obsolete, or at least obsolescent among chemists, just as the terms invertebrate and cryptogam have become obsolete in classification among biologists. The latter words are still popularly used because they conveniently indicate, in a very general way, a vast number of beings, which however have little in common except negative characters. Organic substances are popularly defined as those produced by the action of living things; but there are now known a multitude of carbon compounds which have not been found in organisms, but are genetically so intimately related to those which have been there produced, that they can not be excluded from the same group. As a single example I may cite the hydrazones,

by means of which sugars of a great variety have been identified and their relationships understood; yet no hydrazone, so far as we know, occurs in plants.

Again: There are many carbon compounds which, normally produced in living beings, have also been produced by synthesis outside the influence of life. As a single example of such I mention oil of wintergreen, which normally occurs in birch bark and wintergreen berries, but which is now produced commercially by synthetic methods. Many other essential oils are likewise manufactured.

Most organic substances therefore belong to a group more correctly known as carbon compounds, whose connection is very intimate. Among these compounds the most stable one, anhydrous carbon dioxide, CO_2, naturally finds a place. It occurs in nature, but is produced also as a result of destructive metabolism in organisms. Heretofore it has been called an inorganic substance. Furthermore, water occurs in nature, but is frequently produced by and in organisms. It too has been called inorganic. But the substances antecedent to these two in the descending scale of oxidation in the organism were called organic. The illogical nature of such a distinction is evident, at least in the case of CO_2.

I do not conceive it to be possible to use the terms organic and inorganic with scientific accuracy, because they are not scientific; but if we endeavor to use them as correctly as our present knowledge demands, we can not say that the food of green plants is inorganic, except in so far as the mineral salts, and possibly the water, are concerned.

This, however, may be considered a mere juggling of words, though I look upon the correct use of words as of especial importance in teaching. I propose to show, however, that neither CO_2, H_2O, nor mineral salts can properly or logically be considered the *food* of green plants.

When these substances are obtained by chlorophyll-bearing cells, as they are from the atmosphere and from the soil respectively, they do not exist as two independent compounds, nor does the CO_2 simply enter into solution in the water. On the contrary a new substance, H_2CO_3, is formed, which is carbonic acid.

Carbonic acid is far more readily decomposable than either of the stable compounds from which it originates. By the action of the protoplasm of the chlorophyll bodies, under the

influence of light of sufficient intensity, this H_2CO_3 is reduced, and a new compound of carbon is formed, of whose nature we are yet ignorant. It is supposed, on various *a priori* and experimental grounds, that this is one of the aldehyde group, probably formic aldehyde, CH_2O. The experiments of Bokorny upon the nutrition of Spirogyra seem to indicate the correctness of this idea. He endeavored to ascertain whether this plant could be supplied with any members of the aldehyde series in solution, and could then continue the same process or produce the same result as when it was supplied with H_2CO_3. Several of the simpler members of the aldehyde group proved deleterious,[2] but direct experiments with methylal ($C_3H_6O_3$) succeeded. This substance was supplied to starved, and hence starch-free, Spirogyra filaments in pure water, and access of CO_2 was prevented. With these conditions, under normal illumination, starch was quickly formed.[3] Not satisfied with this however, Bokorny succeeded[4] in obtaining the same result under similar conditions by using a nutrient solution containing 1:100 or 1:1000 of sodium oxymethylsulphonate, CH_3NaSO_4, which easily decomposes at a low temperature into formic aldehyde and sodic sulphite, $CH_2O+NaHSO_3$. Boehm's experiments with cane sugar[5] and, later, Arthur Meyer's[6] with levulose, dextrose, galactose, mannite and glycerin, show that the ordinary parenchyma cells of the green leaf can form starch from solutions of these substances supplied to starved (starch-free) leaves.

In view of these results, which do not stand alone, and are also supported by E. Fischer's work on the synthesis of sugars,[7] it can hardly be doubted that complex carbon compounds

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[2]LOEW und BOKORNY: Chem.-physiol. Studien über Algen. Jour. f. pract. Chem. XXXVI (1887). 272–291.

[2]BOKORNY: Ueber Stärkebildung aus verschiedenen Stoffe. Ber. d. deutsch. bot. Gesells. VI (1888). 116–120. See also his Welche Stoffen können ausser Kohlensäure zur Stärkebildung in grünen Pflanzen dienen? Landw. Vers. Stat. XXXVI (1889). 229–242.

[4]BOKORNY: Ueber Stärkebildung aus Formaldehyde. Ber. d. deutsch. bot. Gesells. IX (1891). 103.

[5]BOEHM: Ueber Stärkebildung aus Zucker. Bot. Zeit. XLI (1883). 33–38, 49–54.

[6]MEYER, A.: Bildung der Stärkekörner in den Laubblättern aus Zuckerarten, Mannit und Glycerin. Bot. Zeit. XLIV (1886). 81–88, 105–113, 129–137, 145–151.—Cf. also LAURENT: Sur la formation d'amidon dans les plantes. Bruxelles, 1888; *fide* Bokorny.

[7]FISCHER, E.: Synthesen in der Zuckergruppe. Ber. d. deutsch. chem. Gesells. XXIII (1890). 2114. See also: Synthese des Traubenzuckers. l. c., p. 779.

arise in the manner indicated by von Baeyer in 1870,[8] viz., by condensation of formic aldehyde. Heretofore, following Sachs' path-breaking researches,[9] it has been believed that starch was not only the first visible product of this process, but that almost or quite all the material manufactured by the chlorophyll body passed at one time or another into the form of starch. The recent work of Brown and Morris,[10] however, proves conclusively that this is not the case. "It is far more probable," they say,[11] "that starch is only elaborated within the cell when the supply of nutriment is in excess of the cell requirements, and that most of the assimilated products never pass through the stage of starch at all." Their experiments "point to the somewhat unexpected conclusion that, at any rate in the leaves of the Tropaeolum, cane sugar is the first sugar to be synthesised." This accumulates in the cell-sap, and when its concentration "exceeds a certain amount . . . starch commences to be elaborated by the chloroplasts." They add: "Our analyses point to the cane sugar being translocated as dextrose and levulose, and the starch as maltose, the latter process only taking place when the starvation of the cell has induced the dissolution of the starch."

The substances standing between formic aldehyde, CH_2O, and the sugars produced by this process are, however, not certainly known, and from the inherent difficulties surrounding the investigation, as well as the instability of the substances themselves, may not be known for a long time.

For our present purpose the only question of importance is whether the C, H, and O are, either in the form of H_2CO_3, or after partial reduction, or in their nascent condition after dissociation, combined with the protoplasm which later forms starch, as is urged by various writers. If they are so combined, then H_2CO_3 must be looked upon as a *food*, and the process be termed assimilation in accordance with long usage in animal physiology.

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[8]BAEYER, A. VON: Ueber die Wasserentziehung und ihre Bedeutung für das Pflanzenleben und die Gährung. Ber. d. deutsch. chem. Gesells. III (1870). 63-75.

[9]SACHS: Ueber den Einfluss des Lichtes auf die Bildung des Amylums in den Chlorophyllkörnern. Bot. Zeit. XX (1862). 365-373.—Also, Ueber die Auflösung und Wiederbildung des Amylums in den Chlorophyllkörnern bei wechselnder Beleuchtung. Bot. Zeit. XXII (1864). 289-294.

[10]BROWN & MORRIS: The chemistry and physiology of foliage leaves. Jour. Chem. Soc. LXIII (1893). 604-677.

[11]Loc. cit. p. 673.

1. Destructive metabolism in plants results in the decomposition of protoplasm, with the production of CO_2 and H_2O. The residue may probably be again combined with C, H, and O, to rebuild protoplasm. Can this be done in the green leaves? Is it accomplished there? For such repair we know that carbohydrates disappear, and that such repair is going on in all living parts, whether green or not. It is conceded that in no part not green could H_2CO_3 be used in this way. Presumptively, therefore, it is not so used in these parts.

2. The amount of H_2CO_3 used by the plant under normal illumination is much greater than necessary to repair waste, and also much greater than the amount necessary to form the starch which appears in the chloroplast. To account for this, on the supposition that starch and similar carbohydrates arise in the chlorophyll body by the actual decomposition of protoplasm, it is necessary to suppose that in the chlorophyll body the protoplasm combines C, H, O, N, and S, at least, *de novo*, to form proteids; or else that the products remaining after the starch is formed from protoplasm are continually rebuilt from the C, H, and O, derived from H_2CO_3. This is a much more complicated process than polymerization of formic aldehyde, and it is by so much more improbable. Moreover it rests, as I believe, upon insufficient observation and faulty deductions from these observations.

Note the point: That carbohydrates *may* arise by the decomposition of protoplasm is, since it is irrelevant, not denied; but that the recomposition, the repair, of the protoplasm so broken down, is accomplished by the direct use of H_2CO_3 is highly improbable.

3. On the view that starch arises only from the decomposition of protoplasm, it is impossible to conceive of any reason why starch is absent from some spermaphytes and from the fungi in general. They are supplied often with food in excess; in favorable circumstances the protoplasm is abundant and active, but however abundant the food or active the protoplasm it never decomposes into starch.

We shall harmonize vegetable physiology best with animal physiology by taking a different view of these processes, one which is not opposed by any observation yet made, so far as I know, and one which is from the chemical side highly probable.

The process in my view is this: Assuming a supply of

CO_2 and H_2O in the presence of chlorophyll bodies furnished with radiant energy of sufficient intensity, there occurs a rearrangement of the molecules of C, H, and O into some simple compound, probably formic aldehyde. By definite changes, probably polymerization, this becomes more and more complex, until finally one of the higher carbohydrates is produced, generally one of the sugars.

I believe that these changes occur through the action of the living protoplasm of the chlorophyll body, but that the H_2CO_3 *is not brought into such relation to the proteid molecules as to form any part of them.* The energy necessary to accomplish the work is supplied in the form of light. The chlorophyll of the chromatophore acts as an absorbent of the rays which are useful in doing the work, as Timiriazeff has shown,[12] and not as a shield.

The process here described has been called "assimilation," "assimilation proper," and "assimilation of carbon." I think that none of these terms is appropriate.[13] Assimilation has been long used in animal physiology to designate the appropriation of digested food by the different tissues, and its conversion into the substances of those tissues. In that general sense it ought to be used in vegetable physiology, or, if it can not be so used, it ought not to be used at all. We have an opportunity to use it so, if we apply it to those changes by which the complex carbon compounds produced by the green cells are appropriated by the various tissues, and made a part of them. Moreover, since in many instances the reserve food is in a solid form, there is in plants a process of *digestion* by which this solid food is altered and dissolved in order that it may be assimilated.

For the process of formation of complex carbon compounds out of simple ones under the influence of light, I propose that the term *photosyntax* be used.[14] The protoplasm, by the

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[12]TIMIRIAZEFF: Enregistrement photographique de la fonction chlorophyllienne par la plante vivant. Compt. Rend. cx (1890). 1346–7.

[13]Cf. WIESNER: Elemente der wiss. Botanik I. 232. "Unter Assimilation versteht man gegenwärtig in der Pflanzenphysiologie die Umwandlung der Kohlensäure und des Wassers in organische Substanz. . . . Diese Auffassung stimmt mit der älteren, in der Thierphysiologie noch immer herrschenden, derzufolge Assimilation die Umwandlung der aufgenommenen Nahrungsmittel in die Bestandtheile der Gewebe bedeutet, nicht überein."

[14]WIESNER: l. c., p. 332: "Es scheint aber bei der im Texte gegebenen Begriffsumgrenzung an einem Worte zu fehlen für jenen wichtigen Process, den man bisher als Assimilation bezeichnete."

aid of light, marshals the molecules into new array and brings bodies of them together into new forms, as the individuals of an army are arrayed in companies, and companies drawn up into regiments. I have carefully considered the etymology and adaptation, as well as the expressiveness, of the word proposed, and consider it preferable to photosynthesis which naturally occurs as a substitute. Its derivation is evident: φως, light; συντασσειν, to put together, to arrange, to organize.

This power, which is possessed by green plants alone, is a power over and above that which any animal possesses, except possibly those which may contain chlorophyll. (In most instances where chlorophyll has been found in animals, it has been shown either to be derived from ingested plants, or to be due to a symbiotic relationship between plants and animals, and all the problematic cases may yet be so solved.)

Much of the food so produced is already in soluble form. But carbohydrate reserve food often appears in solid form, particularly of starch and cellulose. How is such food utilized? Manifestly there must first be its alteration into a soluble condition. This is accomplished by the agency of alterative enzymes. From the action of diastase on starch a sugar, maltose, results, which may be translocated and utilized directly in repair and growth. Cellulose is altered and dissolved likewise. Even the already soluble cane sugar produced by photosyntax needs to be changed into dextrose and levulose in order to be translocated readily. What are these changes but *digestion?*

Under this view the nutrition of green plants resolves itself into three processes, photosyntax, digestion, and assimilation. Photosyntax deals only with carbohydrates; digestion and assimilation with all classes of foods.

Photosyntax is the synthesis of complex carbon compounds out of carbonic acid, in the presence of chlorophyll, under the action of light.

Digestion consists in chemical change and solution of the solid foods. It is due in large measure, perhaps entirely, to the action of alterative enzymes.

Assimilation is the conversion of the foods into the living or mechanical substances of the plant tissues for repair of waste and growth.

Food is the physiological term for all substances capable of

direct assimilation or of digestion and assimilation. It includes the carbon compounds produced by photosyntax and many other substances, but is not applicable to CO_2 and H_2O, which are built into carbohydrates.

By these slight yet important changes in terminology we bring ourselves into harmony with the present knowledge of animal physiology, and have a much more intelligible and intelligent point of view from which to discern further truths regarding plant nutrition.

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The bacterial flora of the Atlantic ocean in the vicinity of Woods Holl, Mass.

A contribution to the morphology and physiology of marine bacteria.

H. L. RUSSELL.

WITH PLATE XXXVI.

(Continued from p. 395.)

General biological features of the different organisms.

Zymogenic properties.

The majority of the bacteria isolated at Woods Holl belong to the liquefying group of micro-organisms and one of their fermentative actions is demonstrated in the production of a peptonizing enzyme that slowly liquefies gelatin. The digestion of the casein in milk cultures also attests the production of ferments that change the insoluble proteids into soluble peptones.

Pathogenic properties.

From the frequency with which bacteria are found in the water and mud of marine areas, it might be presumed that the organisms in question had no pathogenic properties but were purely saprophytic in their nutritive adaptation. This presumption however is not warranted on *a priori* grounds and it becomes necessary in working out the full life history of a micro-organism to test the relation of the germ as to its pathogenic properties. For this purpose, white rats were inoculated with one cc. of freshly grown bouillon cultures of the